

# Changes in the Ratio of Plants with Different Mycorrhizal Status in the Course of Pasture Digression in the Southern Ural Steppes

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**Abstract**—Trends in the proportions of plants differently interacting with mycorrhizal fungi in the course of pasture digression have been analyzed in the steppe zone of the Southern Urals. Estimates of species richness and abundance of plant groups with different mycorrhizal status have been obtained by comparing original data on the structure of phytocenoses with published data on the ability of plant species to form mycorrhizae. It has been shown that the proportions and abundance of obligate mycorrhizal species decrease significantly in the course of digression, with consequent increase in those of species less dependent on or independent of symbiosis with fungi, i.e., facultative mycorrhizal or obligate nonmycorrhizal plants.

**Keywords:** vegetation succession, grazing, pasture digression, steppe zone, mycorrhizal symbiosis, arbuscular mycorrhiza, mycorrhizal plants, nonmycorrhizal plants, plant strategies

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The study of trends in the transformation of herbaceous ecosystems (steppes and meadows) under the impact of herbivores is a traditional, but still relevant, line of research in the ecology of terrestrial ecosystems and geobotany. Although pertinent publications are numerous, they basically concern three subject matters. The first is identification and phytocenotic characterization of stages in pasture digression, which are usually performed to estimate the optimal or economically expedient grazing intensity. The second is analysis of the mechanisms of rearrangements in phytocenoses and ecosystems under grazing load, including changes in the bioecological properties of plants and transformation of other biotic and abiotic components of ecosystems. The third is experimental research aimed, in particular, at finding ways to sustainable management of rangelands and improvement of their state.

This study falls into the second category, since it deals with changes in the occurrence and abundance of plants differently interacting with arbuscular mycorrhizal fungi in the course of pasture digression in steppe plant communities. Such a study appears relevant in view of the increasing amount of data on the possible role of mycorrhizal symbioses in the dynamics of vegetation. It has been shown experimentally that the outcome of competition between plants largely depends on their predisposition to and success in symbiotic interaction with mycorrhizal fungi (Heijden et al., 1998, 2003; Pezzani et al., 2006; Püschel, Ryd-

lova, and Vosatka, 2007). This finding is confirmed by data on the increasing closeness of mycorrhizal relationships and the importance of mycotrophic nutrition for plants in the course of progressive endoecogenetic successions (Miller, 1979; Gemma and Koske, 1990; Jumpponen et al., 2002; Ahlu et al., 2005; Pezzani et al., 2006; Lambers et al., 2008). Identification of specific features of mycorrhiza formation in plant communities disturbed by grazing may provide a deeper insight into the mechanisms of their transformation by making it possible to analyze relationships at the ecosystem level, i.e., between the soil and organisms of different trophic levels: autotrophic plants, large herbivorous animals, and soil heterotrophs.

## STUDY REGION AND METHODS

Studies were performed in the region of Guberlinski Hillocks, the Southern Urals (Gaikii raion of Orenburg oblast; 51°07'–51°10' N, 57°50'–58°03' E). The area is strongly dissected by deep stream valleys and ravines. Watersheds contain numerous rocky hills with screes on slopes, which rise up to 360–440 m a.s.l., or 200–250 m above the water level in the Ural River. The climate of the region is sharply continental, with monthly average temperatures of –15.4°C in January and 22.2°C in July and annual average precipitation of 280–310 mm. The soil moisture regime is unstable, and the probability of drought is 30–40%. Because of dissected topography, the soil cover is heterogeneous:

**Table 1.** Initial plant formation, ecotope conditions, and numbers of test plots in geobotanical transects (from Morozova, 1988)

Transect no.	Initial plant formation, soils, and topographic position	Number of plots at the corresponding stage of digression				Number of species per transect
		I	II	III	IV	
1	Feather grass ( <i>Stipa zalesskii</i> Wilenski)—meadow grass ( <i>Poa transbaicalica</i> Roshev.) bunch-grass steppes on shallow (< 40 cm) southern calcareous chernozems in slight depressions on southeastern slopes	1	2	1	1	97
2	Desert oat grass ( <i>Helictotrichon desertorum</i> (Less.) Nevski) bunch-grass steppes on shallow (< 30 cm) southern calcareous chernozems in smooth northern slopes	2	1	1	1	95
3	Feather grass ( <i>Stipa lessengiana</i> Trin. & Rupr.)—sheep's fescue ( <i>Festuca valesiaca</i> Gaudin) bunch-grass steppes on shallow (< 30 cm) southern calcareous chernozems on southwestern foreslopes	1	1	1	1	44
4	Mixed petrophyte ( <i>Festuca valesiaca</i> Gaudin + <i>Potentilla arenaria</i> Borkh.) stony steppes on poorly developed gravely stony soils at the hilltops	1	no	1	1	64

For description of digression stages (I–IV), see the text.

southern calcareous chernozems prevail in level areas; southern chernozems with different degrees of erosion, on slopes; poorly developed medium gravel soils with rock outcrops, on topographic highs; and meadow chernozem and soddy meadow–forest soils, in topographic lows. The zonal vegetation is represented by true bunch-grass steppe communities, but the diversity of topographic forms accounts for a patchwork pattern of plant cover, which changes depending on slope angle and aspect, bedrock composition, and soil depth.

Phytocenotic analysis of pasture digression of steppe communities exposed to goat grazing was performed in 1982 to 1985 in four ecotopographic transects, three in true bunch-grass steppes on slopes of different aspects and one in stony steppes, along topographic highs. The transects were arranged so as to reveal specific features of degradation of true bunch-grass steppe communities formed by different steppe grass species in different ecotopes (Table 1). Each transect consisted of three to five 10 × 10-m plots located at different distances from goat barns or pens and, therefore, differently affected by grazing. During the study period, grazing load exceeded the optimal level by a factor of four to six (Morozova, 1985, 1991). In each plot, geobotanical relevés were made and the abundance of all plant species (on the Drude scale) was recorded several times per growing season over 3–4 years.

The following stages of digression were distinguished in the plots: (I) background plots, including those used for hay harvesting but not for grazing; (II) slightly or (III) moderately disturbed; and

(IV) severely disturbed and completely overgrazed plots. During data analysis, slightly and moderately disturbed plots (II + III) were considered together, since we failed to find stage II communities at the hilltops along the stony steppe transect. Slightly disturbed communities are absent in this digression series because of specific conditions in corresponding ecotopes, where the vegetation is overgrazed much more rapidly than in the true bunch-grass steppes.

The mycorrhizal status of plants was determined on the basis of published data, using the maximum possible number of publications on each species. On the whole, about 30 published sources were used, including papers by teams of botanists from Perm (headed by I.A. Selivanov) and Yekaterinburg (headed by T.S. Chibrik), L.M. Nozadze's studies, and reviews by Harley and Harley (1987) and Wang and Qiu (2006). Species in which no mycorrhiza was found by any of the authors were classified as nonmycorrhizal. Species regarded as mycorrhizal in some publications and as nonmycorrhizal in other publications were classified as facultative mycorrhizal. Species described as forming arbuscular mycorrhizae in all available published sources were classified as obligate mycorrhizal. Plant species names are given according to Cherepanov (1995).

The significance of differences in the occurrence and abundance of species differing in mycorrhizal status was evaluated by two-way ANOVA, with arcsine transformation of percentage data. The test character value in a plot was taken as an accounting unit. Grades of plant abundance on the Drude scale were converted

into percent coverage, taking that sol = 1%, sp = 5%, cop<sub>1</sub> = 15%, cop<sub>2</sub> = 33%, and cop<sub>3</sub> = 75%.

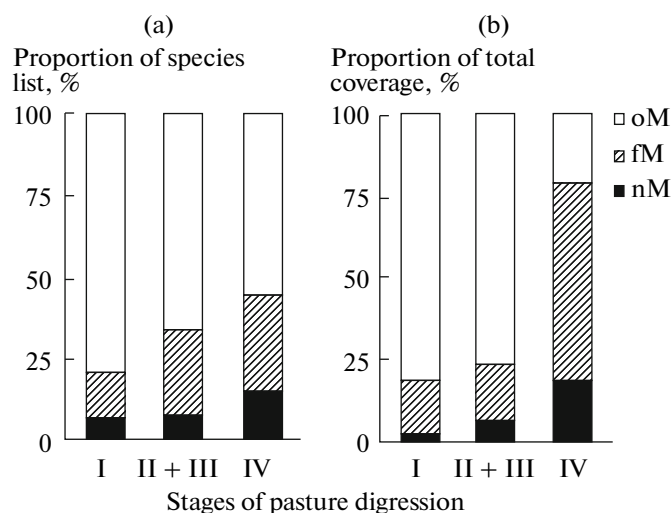
## RESULTS AND DISCUSSION

A total of 132 species were recorded in 17 test plots, and the mycorrhizal status was determined for 101 species. They included 10 nonmycorrhizal and 16 facultative mycorrhizal plants, while the greater part of species (75) proved to be obligate mycorrhizal. No data on the ability to form mycorrhizal symbiosis were found for 31 species (23% of the total number). Such a major proportion of species could not be a priori excluded from consideration, and the first stage of analysis was performed with the entire data set (132 species).

A series of ANOVA tests were carried out to characterize two sources of variation in the species richness and coverage of species groups differing in mycorrhizal status, namely, differences between communities at different stages of digression and differences between communities occupying different topographic positions (Table 2). Before analyzing changes in the ratio of plants with different mycorrhizal status, it should be noted that the total number of species in the relevés and their coverage proved to vary significantly depending only on the factor "grazing load," decreasing in strongly disturbed plots, but did not vary between the transects (i.e., between different topographic locations).

Obligate mycorrhizal species constitute the floristic and phytocenotic core of undisturbed phytocenoses, accounting for 60–90% of species lists and 70–95% of total plant coverage in corresponding plots. In particular, this group includes typical steppe dominants such as *Achillea nobilis* L., *Festuca rupicola* Heuff., *F. valesiaca* Gaudin, *Galatella villosa* (L.) Rchb., *Stipa lessingiana* Trin. & Rupr., *S. tirsia* Steven, *S. zaleskii* Wilensky, and *Thymus marschallianus* Willd. On average, the number of obligate mycorrhizal species per relevé and their proportion in species lists decrease under grazing load by factors of 3.3 and 1.5, respectively. The total abundance of these species also decreases significantly: in strongly disturbed plots, their absolute coverage is 9.3 times lower than in undisturbed communities, and their contribution to the total coverage of phytocenoses is 3.4 times lower. Thus, heavy grazing load creates unfavorable conditions for obligate mycorrhizal plants.

In contrast, the response of facultative mycorrhizal plants to increasing grazing load is more positive than negative. This group includes typical ruderal plants that are common or even abundant in areas exposed to intensive grazing, such as *Capsella bursa-pastoris* (L.) Medikus, *Ceratocephala testiculata* (Crantz) Besser, *Chenopodium album* L., *Eremopyrum orientale* (L.) Jaub. & Spach, *Polygonum aviculare* L., and *Setaria viridis* (L.) P. Beauv. The proportion of facultative mycorrhizal plants in species lists and their contribution to the total coverage are 2.1 and 3.7 times higher,



Contributions of (nM) nonmycorrhizal, (fM) facultative mycorrhizal, and (oM) obligate mycorrhizal species to (a) species composition and (b) total plant coverage of plots at different stages of pasture digression.

respectively, in strongly disturbed than in undisturbed areas. They are most abundant in plots at stage IV of digression, where they account for 35–70% of the total plant coverage, compared to only 2–20% in undisturbed steppe plots.

Nonmycorrhizal species are a minor component of steppe phytocenoses. As a rule, this group in a plot is represented by no more than 2–3 species. Their number does not change significantly in the course of digression, but the proportion of nonmycorrhizal species in phytocenosis increases significantly, from 0–8% to 6–23% of the total species list. Thus, it appears that nonmycorrhizal plants in general positively respond to intensification of grazing, as follows from an increase in their absolute and relative coverage in disturbed communities. However, plants of this group are ecologically heterogeneous, and, in fact, only the annual *Ceratocarpus arenarius* L. becomes significantly more abundant in overgrazed plots, while other species (e.g. *Caragana frutex* (L.) K. Koch) have low abundance either in disturbed or in background communities. It has been found that *Eremogone longifolia* (M. Bieb.) Fenzl and *Euphrasia pectinata* Ten. are absent in moderately and strongly disturbed plots, while segetal species *Amaranthus retroflexus* L. and *Chenopodium acuminatum* Willd. occur only in areas under high grazing load.

The distribution of species with an indeterminate mycorrhizal status does not depend on grazing load. In particular, neither the absolute number of such species (on average, 3–8 per plot) nor their proportion (on average, 15–21% of the total species list) change between the stages of digression. On the other hand, their occurrence and abundance distribution appear to correlate with the topographic position of the plot. In

**Table 2.** Average species richness and coverage ( $m \pm SE$ ) of plant groups differing in mycorrhizal status at different stages of pastoral digression and estimates of the significance of different variation sources

Species group	Digression stages*			Variation sources**				
	I	II + III	IV	[1] grazing load ( <i>df</i> = 2)		[2] topographic position ( <i>df</i> = 3)		[1] × [2] ( <i>df</i> = 3)
				<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	
Number of species on the list								
Obligate mycorrhizal	31.6 ± 3.5	16.4 ± 1.8	9.5 ± 2.1	26.29	0.0022	3.60	0.1008	1.36
Facultative mycorrhizal	5.6 ± 1.1	6.5 ± 0.6	5.0 ± 1.7	1.18	0.3797	3.73	0.0952	1.68
Nonmycorrhizal	2.6 ± 0.8	1.8 ± 0.4	2.5 ± 0.6	2.59	0.1693	8.90	0.0190	1.27
Species of indeterminate status	8.2 ± 2.3	6.3 ± 0.9	3.3 ± 1.0	5.07	0.0626	6.39	0.0366	1.41
Total	48.0 ± 7.2	31.0 ± 2.9	20.3 ± 4.4	11.96	0.0124	5.17	0.0544	1.38
Proportion in species list, %								
Obligate mycorrhizal	68.8 ± 5.7	52.5 ± 1.7	46.9 ± 6.4	51.18	0.0005	21.60	0.0027	8.45
Facultative mycorrhizal	11.3 ± 1.0	21.4 ± 1.8	23.9 ± 4.6	6.34	0.0425	1.27	0.3799	0.81
Nonmycorrhizal	4.7 ± 1.3	5.6 ± 0.9	13.2 ± 3.6	155.17	0.0000	89.33	0.0001	19.42
Species of indeterminate status	15.2 ± 4.3	20.5 ± 2.0	16.0 ± 4.5	2.40	0.1862	6.41	0.0364	1.30
Coverage, %								
Obligate mycorrhizal	102 ± 10	59 ± 5	11 ± 3	21.66	0.0034	0.48	0.7125	0.56
Facultative mycorrhizal	21 ± 8	13 ± 3	31 ± 9	8.09	0.0271	12.25	0.0097	1.03
Nonmycorrhizal	3 ± 1	5 ± 2	10 ± 5	2.05	0.2239	2.04	0.2267	1.36
Species of indeterminate status	9 ± 3	8 ± 3	9 ± 3	0.72	0.5294	13.10	0.0084	5.69
Total coverage	135 ± 20	85 ± 6	61 ± 14	7.55	0.0309	3.19	0.1219	0.84
Contribution to total coverage, %								
Obligate mycorrhizal	78.3 ± 5.1	69.8 ± 3.7	22.8 ± 8.3	39.67	0.0009	3.01	0.1329	1.32
Facultative mycorrhizal	13.3 ± 4.0	14.8 ± 2.8	49.6 ± 7.7	86.44	0.0001	15.20	0.0060	2.62
Nonmycorrhizal	1.8 ± 0.4	5.7 ± 2.6	13.9 ± 5.9	2.98	0.1406	1.57	0.3074	0.79
Species of indeterminate status	6.6 ± 2.3	9.7 ± 2.9	13.7 ± 4.1	5.46	0.0552	15.74	0.0056	3.22
								0.1099

\* For description of digression stages (I–IV), see the text.

\*\* ( $df$ ) Degrees of freedom, ( $F$ ) Fisher's test, ( $P$ ) significance level.

particular, relatively many species of this group grow in stony steppes on the hilltops, and parameters of their abundance in these biotopes are also higher. A probable explanation to this situation is that the vegetation of stony steppes and rock outcrops is relatively rich in plants that have not been previously analyzed for mycorrhiza formation (e.g., rare of small-range species).

The fact that species with an indeterminate mycorrhizal status are not generally confined to communities with a certain degree of disturbance is important in methodological terms: on this basis, such species can be reasonably excluded from consideration in formulating the answer to the main question, i.e., how the occurrence of species differing in mycorrhizal status changes in the course of pastoral digression. The answer that follows from the data presented above is unequivocal: intensification of grazing leads to a decrease in representation and abundance of species that can successfully develop only upon forming symbiosis with arbuscular mycorrhizal fungi, with consequent increase in corresponding parameters of species that are less dependent on such symbiosis (facultative mycorrhizal and nonmycorrhizal plants) (figure).

The main trends in the transformation of vegetation under grazing load in the study region are expectable. In agreement with previous data (Morozova, 1985, 1990, 1991) they include a decrease in the species richness and productivity of phytocenoses, with the spectrum of life forms and types of plant ontogeny shifting in favor of monocentric annual and biennial species of ruderal type. Another phenomenon accompanying pastoral digression of the steppe vegetation is the weakening of mycorrhizal interactions. Under intensive grazing, when the structure of phytocenoses is generally simplified, advantage is gained by plants that can develop without mycorrhizae. This situation is inverse to that of increase in the proportion of mycorrhizal plants upon structural complication of phytocenoses in the course of natural endoecogenetic successions (Miller, 1979; Gemma and Koske, 1990; Ahulu et al., 2005; Püschel et al., 2007) and, hence, is somewhat predictable. It can be explained by assuming that the type of plant strategy determining the position of species in succession is correlated with their mycorrhizal status. The positive correlation of the ruderal ecological strategy, whose particular distinctive features include a short ontogeny or a high reproductive effort (Grime et al., 1988), with the avoidance of mycorrhizal symbiosis has been discussed previously (Grime et al., 1988; Francis and Read, 1995; Cornelissen et al., 2001; Betekhtina and Veselkin, 2011). The decrease in the proportion of mycorrhizal species in favor of nonmycorrhizal species in the course of pastoral succession indicates that the ability of plants to form mycorrhizal symbiosis positively correlates with their competitiveness in the absence of grazing load and negatively correlates with their ability to grow under conditions of overgrazing.

It appears that changes in the ratio of mycorrhizal and nonmycorrhizal plants are accompanied by rearrangements in the communities of symbiotic arbuscular fungi. Reduction in the amount of resources (products of plant photosynthesis) available to these fungi in overgrazed areas should have an adverse effect on the abundance and, probably, composition of their populations. In turn, multiple trophic and regulatory interrelations between arbuscular fungi and other groups of soil biota (Coleman, 2008) imply that disturbances in mycorrhizal interactions may be responsible for other rearrangements in the ecosystem. At present there is no sufficient basis to discuss such rearrangements, but it would be interesting to estimate the extent of transformation of ecosystem processes that results from changes in the prevailing ways of soil nutrient consumption by plants under grazing load.

On the whole, the presented data on changes in the ratio of plants differing in mycorrhizal status under the impact of goat grazing provide a somewhat new insight into factors responsible for changes in plant communities in the course of pastoral digression. They confirm the opinion that giving consideration to plant mycorrhizal status can provide for better understanding of certain ecological features of plants and their communities (Mukhin and Veselkin, 2004). In view of this, the digressive succession considered in the study may be described as follows: under conditions of intensive goat grazing in the true bunch-grass and stony steppes, polycentric perennial, obligate mycorrhizal plants characterized by vegetative stability and high above- and belowground biomass production are largely replaced by monocentric annual and biennial plants with a low biomass, which are mostly nonmycorrhizal or facultative mycorrhizal.

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